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Termite mounds harness diurnal temperature oscillations for ventilation

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Many species of millimetric fungus-harvesting termites collectively build uninhabited, massive mound structures enclosing a network of broad tunnels that protrude from the ground meters above their subterranean nests. It is widely accepted that the purpose of these mounds is to give the colony a controlled microclimate in which to raise fungus and brood by managing heat, humidity, and respiratory gas exchange. Although different hypotheses such as steady and fluctuating external wind and internal metabolic heating have been proposed for ventilating the mound, the absence of direct in situ measurement of internal air flows has precluded a definitive mechanism for this critical physiological function. By measuring diurnal variations in flow through the surface conduits of the mounds of the species *Odontotermes obesus*, we show that a simple combination of geometry, heterogeneous thermal mass, and porosity allows the mounds to use diurnal ambient temperature oscillations for ventilation. In particular, the thin outer flutelike conduits heat up rapidly during the day relative to the deeper chimneys, pushing air up the flutes and down the chimney in a closed convection cell, with the converse situation at night. These cyclic flows in the mound flush out CO₂ from the nest and ventilate the colony, in an unusual example of deriving useful work from thermal oscillations.

termite mound | ecosystem engineering | ventilation | niche construction | thermodynamics

Many social insects that live in dense colonies (1, 2) face the problem of keeping temperature, respiratory gas, and moisture levels within tolerable ranges. They solve this problem by using naturally available structures or building their own nests, mounds, or bivouacs (3). A particularly impressive example of insect architecture is found in fungus-cultivating termites of the subfamily Macrotermitinae, individually only a few millimeters in body length, which are well known for their ability to build massive, complex structures (4, 5) without central decision-making authority (6). The resulting structure includes a subterranean nest containing brood and symbiotic fungus, and a mound extending ~ 1–2 m above ground, which is primarily entered for construction and repair, but otherwise relatively uninhabited. The mound contains conduits that are many times larger than a termite (5), and viewed widely as a means to ventilate the nest (7). However, the mechanism by which it works continues to be debated (8–11).

Ventilation necessarily involves two steps: transport of gas from underground metabolic sources to the mound surface, and transfer of gas across the porous exterior walls with the environment. Although diffusion can equilibrate gradients across the mound surface (12), it does not suffice to transport gas between nest and surface. (It takes gas ~ 4 d to diffuse 2 m.) Thus, ventilation must rely on bulk flow inside the mound. Previous studies of mound-building termites have suggested either thermal buoyancy or external wind as possible drivers, making a further distinction between steady [e.g., metabolic driving (11), steady wind] and transient [e.g., diurnal driving (9, 10), turbulent wind (8)] sources. However, the technical difficulties of direct in situ measurements of airflow in an intact mound and its correlation with internal and external environmental conditions have precluded differentiating between any of these

hypotheses. Here, we use both structural and dynamic measurements to resolve this question by focusing on the mounds of *O. obesus* (Termitidae, Macrotermitinae), which is common in southern Asia in a variety of habitats (13).

In Fig. 1A, we show the external geometry of a typical *O. obesus* mound, with its characteristic buttresslike structures (flutes) that extend radially from the center (Fig. 1B). The internal structure of the mound can be visualized using by either making a horizontal cut (Fig. 1C) or endocasting (Fig. 1D). Both approaches show the basic design motif of a large central chimney with many surface conduits in the flutes; all conduits are larger than termites, most are vertically oriented, and well connected. (A simple proof of well connectedness is that gypsum injected from a single point can fill all interior conduits.) This macroporous structure can admit bulk internal flow and thus could serve as an external lung for the symbiotic termite–fungus colony.

To understand how the mound interacts with the environment, we first note that the walls are made of densely deposited granules of clay soil, forming a material with high porosity (37–47% air, by volume; *SI Appendix*), and small average pore diameter (~ 5 μm, roughly the mean particle size). Indeed, healthy mounds have no visible holes to the exterior, and repairs are quickly made if the surface is breached. The high porosity means that the mound walls provide little resistance to diffusive transport of gases along concentration gradients. However, the small pore size makes the mound very resistant to pressure-driven bulk flow across its thickness. Thus, the mound surface behaves like a breathable wind-breaker. Finally, the low wind speeds observed around the termite mounds of ~ 0–5 m/s implies that they are not capable of creating

Significance

Termite mounds are meter-sized structures built by millimeter-sized insects. These structures provide climate-controlled microhabitats that buffer the organisms from strong environmental fluctuations and allow them to exchange energy, information, and matter with the outside world. By directly measuring the flow inside a mound, we show that diurnal ambient temperature oscillations drive cyclic flows that flush out CO₂ from the nest and ventilate the mound. This swarm-built architecture demonstrates how work can be derived from the fluctuations of an intensive environmental parameter, and might serve as an inspiration and model for the design of passive, sustainable human architecture.

Author contributions: L.M. conceived research; H.K., S.O., and L.M. designed research; H.K. and S.O. performed research; H.K. and S.O. contributed new reagents/analytic tools; H.K., S.O., and L.M. analyzed data; and H.K., S.O., and L.M. wrote the paper.

The authors declare no conflict of interest.

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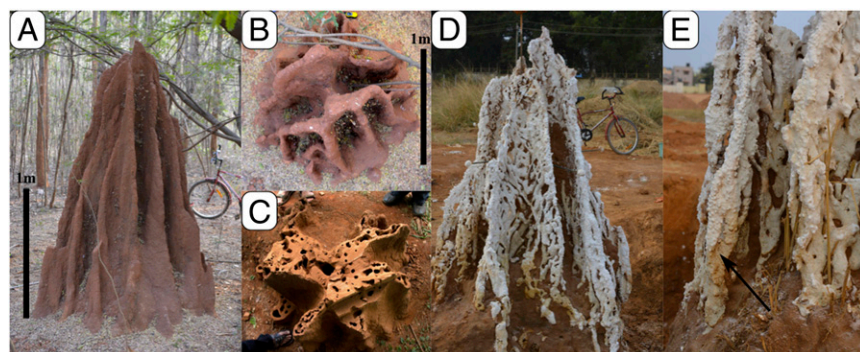


Fig. 1. Mounds of *O. obesus*. Viewed from (A) the side, (B) top, and by (C) cross-section. Filling the mound with gypsum, letting it set, and washing away the original material reveals the interior volume (white regions) as a continuous network of conduits, shown in D. Endocast of characteristic vertical conduit in which flow measurements were performed, near ground level, toward the end of flutes, indicated by the arrow (E).

significant bulk flow across the wall, effectively ruling out wind as the primary driving source.

Within the mound, a range of indirect measurements of CO_2 concentration, local temperature, condensation, and tracer gas pulse chase (8–10, 11, 14) show the presence of transport and mixing. However, a complete understanding of the driving mechanism behind these processes requires direct measurements of flow inside the mound. This is difficult for several reasons. First, the mound is opaque, so that any instrument must be at least partly intrusive. Second, expected flows are small (\approx centimeters per second), outside the operating range of commercial sensors, requiring a custom-engineered device. Third, because conduits are vertical, devices relying on heat dissipation, or larger, high heat capacity setups can generate their own buoyancy-driven (and geometry dependent) flows, making measurements ambiguous (15). Finally, and most importantly, the mound environment is hostile and dynamic. Termites tend to attack and deposit sticky construction material on any foreign object, often within 10 min of entry. If one inserts a sensor even briefly, termites continue construction for hours, effectively changing the geometry and hence the flow in the vicinity of the sensor.

To measure airflow directly, we designed and built a directional flow sensor composed of three linearly arranged glass bead thermistors, exposed to the air (SI Appendix). A brief pulse of current through the center bead creates a tiny bolus of warm air, which diffuses outward and is measured in either neighboring bead. (The operating mechanism is similar in principle to that of ref. 16.) Directional flow along the axis of the beads biases this diffusion, and is quantified by the ratio of the maximum response on each bead, measured as a temperature-dependent resistance. In a roughly conduit-sized vertical tube, this resistance-change metric depends linearly on flow velocity, with a slight upward bias due to thermal buoyancy. This allows us to measure both flow speed and direction locally. The symmetry of the probe allows for independent calibration and measurement in two orientations by rotating by 180° (arbitrarily labeled upward and downward; SI Appendix).

In live mounds, the sensor was placed in a surface conduit at the base of a flute for $\lesssim 5$ min at a time to avoid termite attacks, which damage the sensors. For a self-check, the sensor was rotated in place, such that a given reading could be compared on both upward and downward calibration curves. We also measured the flow inside an abandoned (dead), unweathered mound that provided an opportunity for long-term monitoring without having termites damage the sensors. Simultaneous complementary measurements of temperature in flutes and the center were taken. To measure the concentrations of CO_2 , a metabolic product, a tube was inserted into the nest; in one mound in the center slightly below ground and another in the chimney at ≈ 1.5 m above. Gas concentration measurements were made every 15 min by drawing a small volume of air through an optical sensor from the two locations for most of one uninterrupted 24-h cycle.

Nearly all of the 25 mounds that were instrumented were in a forest with little direct sunlight. In Fig. 24, we show flow measurements in 78 individual flutes of these mounds as a function of time of day. We see a clear trend of slight upward (positive) flow in the flutes during the day, and significant downward (negative) flow at night. The data saturates for many night values, as the flow speed was larger than our range of reliable calibration (SI Appendix). In Fig. 2B, we show the flow rate for a sample flute in the abandoned mound. Notably, it follows the same trend seen in live mounds, but the flow speeds at night are not nearly as large as for the live mounds. For both live and dead mounds, we also show the

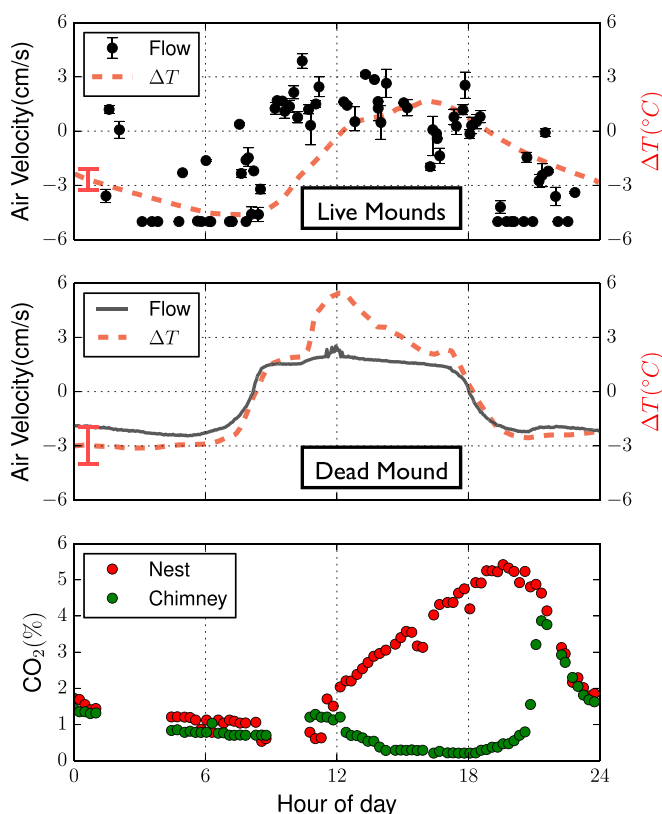
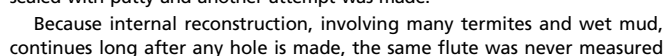


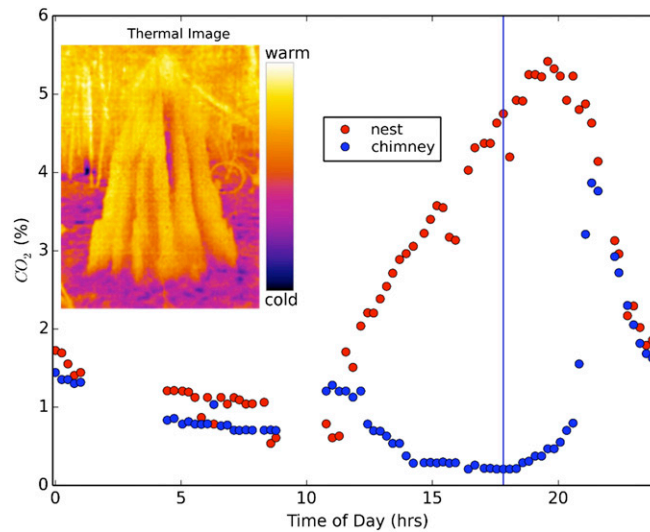
Fig. 2. Diurnal temperature and flow profiles show diurnal oscillations. (Top) Scatterplot of air velocity in individual flutes of 25 different live mounds (\bullet). Error bars represent deviation between upward and downward ≈ 1.5 -min flow measurements. The dashed red line is the average difference between temperatures measured in four flutes and the center (at a similar height), ΔT , in a sample live mound (Representative error bar shown at left). (Middle) Corresponding flow and ΔT , continuously measured in the abandoned mound. (Bottom) CO_2 schedule in the nest (\bullet) and the chimney 1.5 m above (\bullet), measured over one cycle in a live mound (Movie S1).



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Supporting Information

King et al. 10.1073/pnas.1423242112



Movie S1. Time-lapse thermal imaging of the mound shows that during the day, the flutes are warmer than the center. This profile is inverted at night. Simultaneous measurements of CO₂ show that it accumulates in the nest during the day and is flushed out when the temperature profile inverts.

[Movie S1](#)

Other Supporting Information Files

[SI Appendix \(PDF\)](#)

Supplementary Information for "Termite mounds harness diurnal temperature oscillations for ventilation"

by H. King, S. Ocko and L. Mahadevan

August 6, 2015

1 Flow Sensor

Our probe consists of three 0.3mm diameter glass coated thermistor beads (Victory engineering corporation, NJ, $R_0 = 20k\Omega$) held exposed by fine leads in a line with 2.5mm spacing. The center bead is used as a heat source, either pulsed or continuous, in steady and transient modes, respectively. As the heat diffuses outward, its bias depends on the direction and magnitude of flow through the sensor, as depicted in Fig. SI.1(Left). The operating principle is similar to that of some sensitive pulsed wire anemometers [1]. Flow is quantified by comparing the signals (effectively temperatures) from either neighboring bead.

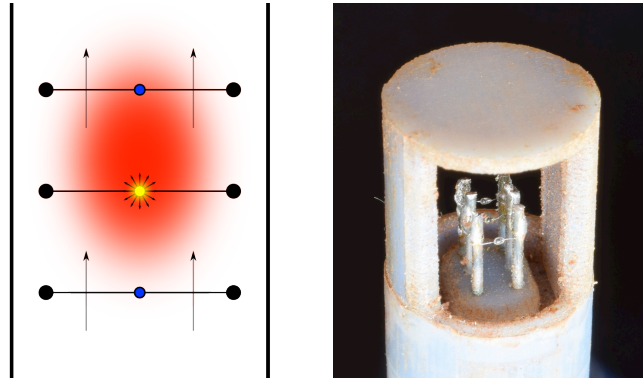


Figure SI.1: Left: Sensor bead schematic. A brief pulse of heat diffuses towards the nearby beads measuring temperature, with a bias in the direction of air flow. Right: Image of the sensor head showing three beads aligned with window of cap.

The plastic housing for the sensor was drawn with Solidworks and printed on a Object Connex500 3D

printer and the individual thermistors were connected to the electronics via shielded Cat 7 ethernet cable. The thermistor beads can be seen in the large window in the protective cap of the sensor in Fig. SI.1(Right).

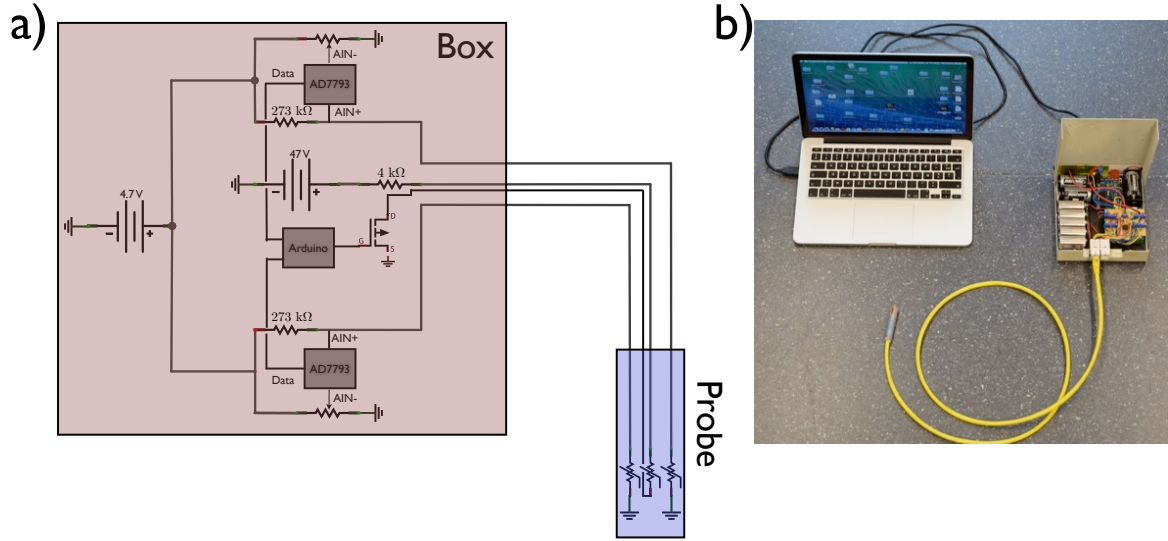


Figure SI.2: a) Schematic of circuit. b) Photograph of setup. The sensor is connected by ethernet cable to the box containing supplemental electronics and Arduino, which is connected to a computer by USB.

1.1 Electronics

Data was collected and the sensor was controlled via an Arduino Uno, while connected to a laptop computer using custom scripts written in Processing. To improve the resolution of the tiny temperature signals, the voltages are measured with AD7793 (Analog Devices) ADCs recording at 10Hz, and a stable baseline signal was supplied by three C batteries in series. The pulsing voltage was supplied by 5 9V batteries, connected momentarily to the middle bead by opening a SIHLZ14 (Vishay) MOSFET. Trimmer potentiometers were used to keep the baseline temperature signal within range of the ADCs. The basic circuit diagram can be seen in Fig. SI.2(a). The supplemental electronics, batteries, and Arduino were housed in a portable metal box, as shown in Fig. SI.2(b).

1.2 Steady mode function

In order to obtain a passive measurement of steady (average) flow, the center bead, in series with 4kΩ was pulsed for 30 ms with 47V every 10 seconds. We estimate its temperature to briefly reach 180 – 300°C. This produced a small bolus of warm air that diffused outward toward neighboring beads in either direction. The tiny change in resistance due to the expanding heat bolus was measured in the neighboring beads, as shown in

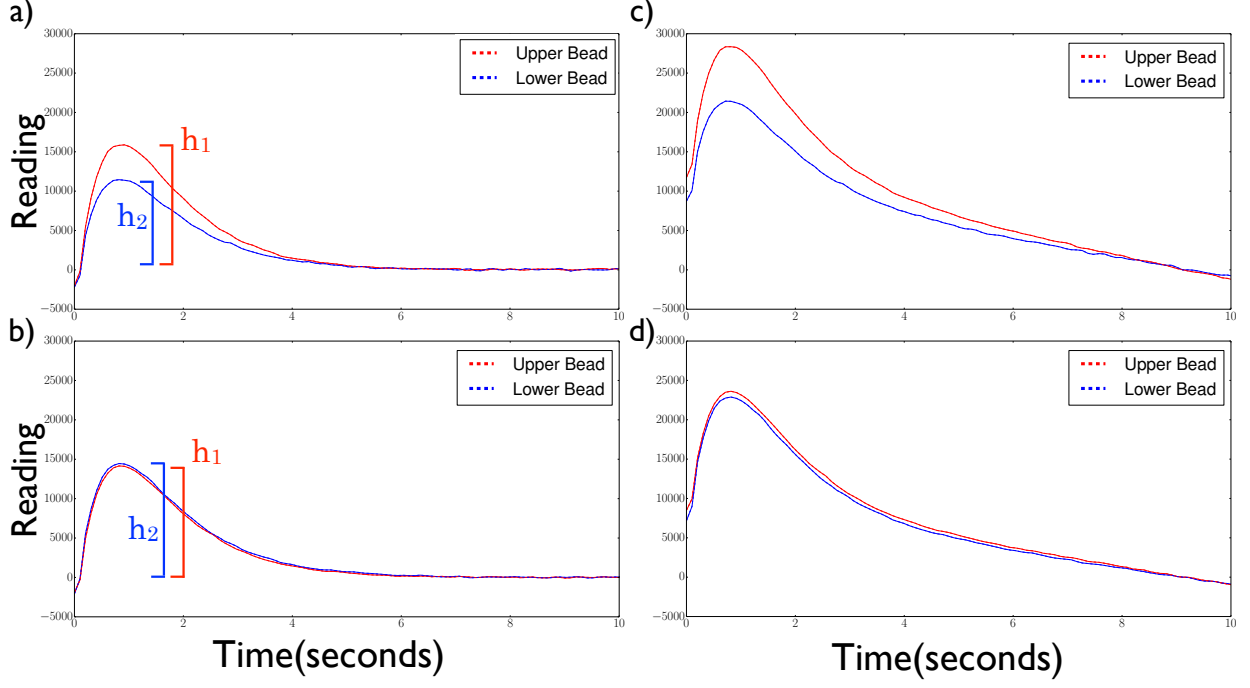


Figure SI.3: Averaged responses from two thermistors as heat bolus diffuses away from center bead for a) Zero flow b) 1.6 cm/s downwards flow in calibration tube. c, d) Averaged responses before subtraction of temperature drift. Probe was intentionally heated before placement in tube for explanatory purposes.

Fig. SI.3. In the absence of flow through the sensor, there is a slight upward bias in the response magnitudes due to thermal buoyancy of the bolus. Upward and downward flow biases the relative responses of the two thermistors in a reproducible way. The log of the ratio of the maxima $\ln(h_1/h_2)$ was used as a metric to calculate flow velocity (see steady flow calibration section). For experimental data sets, temperature drift must be subtracted as the probe equilibrates with the interior flute temperature.

1.3 Transient mode function

While in steady mode, infrequent, brief pulsing of heat avoids troublesome induced convective currents, it prohibits measurement of high frequency ($\gtrsim .1$ Hz) changes in flow. In transient mode of the same sensor, continuous voltage 47 V is applied across the middle bead, such that transients in the flows can be measured from the instantaneous ratio of responses in the neighboring beads. The trade-off is that information about the baseline flow is lost, because induced currents, which depend on several parameters, including unknown details of tunnel geometry, can dominate the signal. Fig. SI.4 shows the response of the neighboring beads in transient mode for some prescribed transients. At ~ 0 cm/s the dependence on the difference between the two readings is the weakest ($\sim \frac{30,000}{\text{cm/s}}$); assuming that slope, the largest fluctuation observed in the field

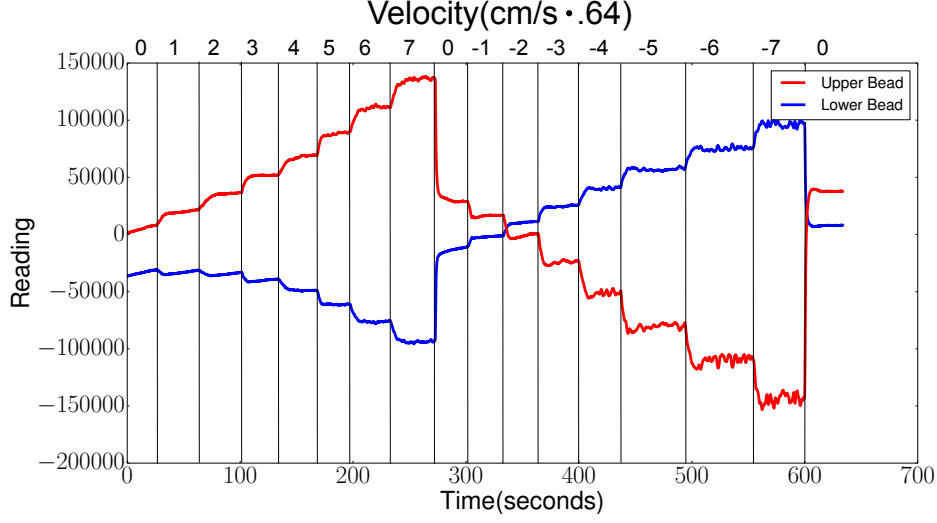


Figure SI.4: Relative readings upper and lower beads in transient mode as flow was varied in increments of .64cm/s

corresponded to $\sim 1mm/s$.

1.4 Steady flow calibration

A 5.6 cm diameter, 2m long, vertical acrylic tube was used as a sample conduit for calibration of the sensor (see Fig. SI.5). The tube was covered with a layer of thermal insulation to prevent external thermal gradients from influencing flow, which was observed when the bottom of the tube was exposed to the sun through a lab window. Air was pulled through the tube by a vacuum source and mass flow controller (Alicat MC-20slpm) in series. To prevent heterogeneous inertial flows where the narrow connector tube met the wider conduit, air was directed through a fine metal mesh before entering a conical flow rectifier. The whole set-up was up-down symmetric, such that by rotating two valves, flow direction could be reversed without changing the setup geometry. The sensor was inserted into a hole in the middle of the tube and oriented so that the beads were aligned with the tube.

As a consistency check and to eliminate possible systematic biases in the probe, every airflow measurement is taken twice using the same probe in two orientations. In one the (arbitrarily named) first bead is above the middle thermistor('upward'); in the other it is directly below ('downward'). To do so, we need separate calibration tables for the 'upward' and 'downward' orientations.

Fig. SI.6 shows the dependence of the metric on flow velocity in the calibration tube. The typical standard deviation between pulses during calibration is small and does not represent the dominant source of error in the field, where variation in conduit geometry plays a larger role (see Experimental Procedure).

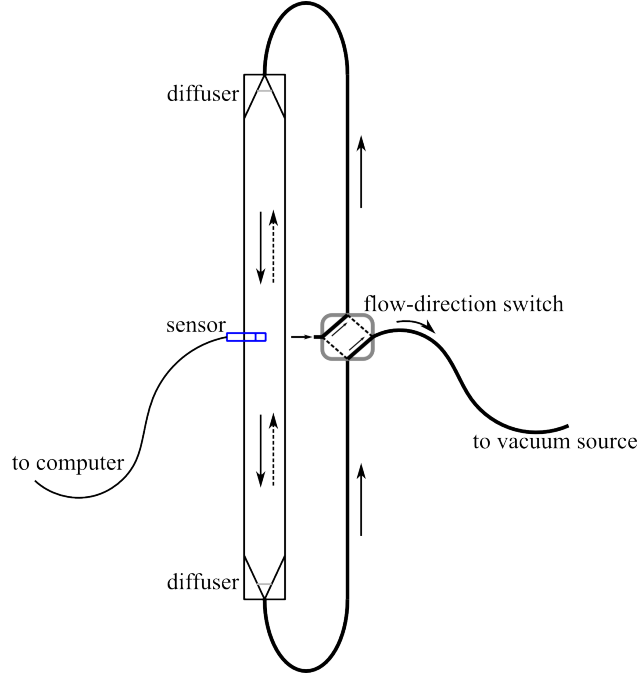


Figure SI.5: Schematic of tube used for calibration. Arrows show direction path of air from inlet toward vacuum source.

There is an unusual, though robust, feature at $\sim \pm 2\text{cm/s}$, where the response briefly jumps. This is most likely an effect due to shifting from a regime of viscously dominated laminar flow to inertial dominated laminar flow. We note that this leads to a small range of flow velocities where we overestimate the flow speed (but not the sign).

Fig. SI.7 shows several calibration curves for the different instances of the sensor, either a spare duplicate sensor, or the same physical sensor after thermistor beads were replaced. Each instance requires a new calibration, as the magnitudes of bead responses varies according to the manufacturer's 25% tolerance, but upon shifting the vertical offset and slope, one can see the qualitative behavior of each instance is the same.

1.5 Temperature and humidity dependence

While the calibration curve in laboratory conditions is robust, additional tests were performed to make sure that our metric was not terribly sensitive to other factors which can vary in the field. Two such factors which should influence the thermal response of the sensor, and therefore its performance are background temperature and humidity. Fig. SI.8 shows the calibration curve for two different ambient temperatures, which roughly represent the range of temperature in the mound. Though the curve has a lower slope at

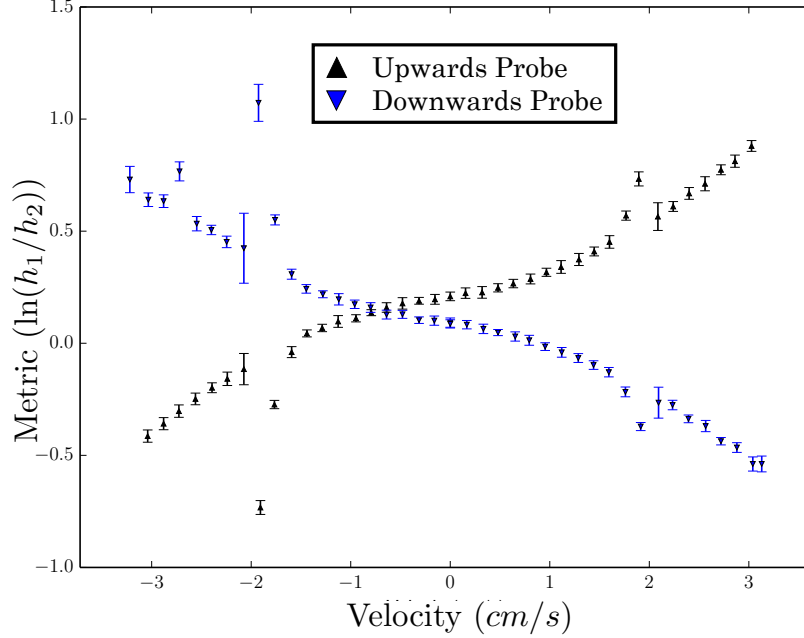


Figure SI.6: Calibration curves for steady flow sensor measured in the plastic tube. The upwards black triangles represent the upwards orientation of the sensor, while the downwards blue triangles represent the downwards orientation. Error bars are the pulse-to-pulse deviation.

higher temperature, which indicates that the sensor underestimates hotter flows, this effect is small compared to the variation of the daily mound flow schedule measured in the field, and would not account for the sign change. The metric, continuously measured for constant flow was unaffected by a change in ambient relative humidity from 25% to 70% (at 29°C).

We can estimate this effect by applying a temperature-dependent calibration, where sensitivity is assumed to vary linearly with temperature, interpolated between the slope and offset of the 21° and 29° curves. Using this with the temperature information from inside the mound, the effect of temperature on all live mound values can be approximated, as shown in Fig. SI.9. We can see the values are only slightly modified, causing a tiny enhancement to the trend, where daytime flows become slightly more positive.

1.6 Orientational Dependence

As mentioned above, the sensor is calibrated exclusively for vertical flow. Though it was not difficult to ensure that local conduit orientation was vertical where the sensor was placed, and that flow was therefore predominantly vertical, it is not unreasonable to suspect that a horizontal flow component could be misinterpreted by the sensor.

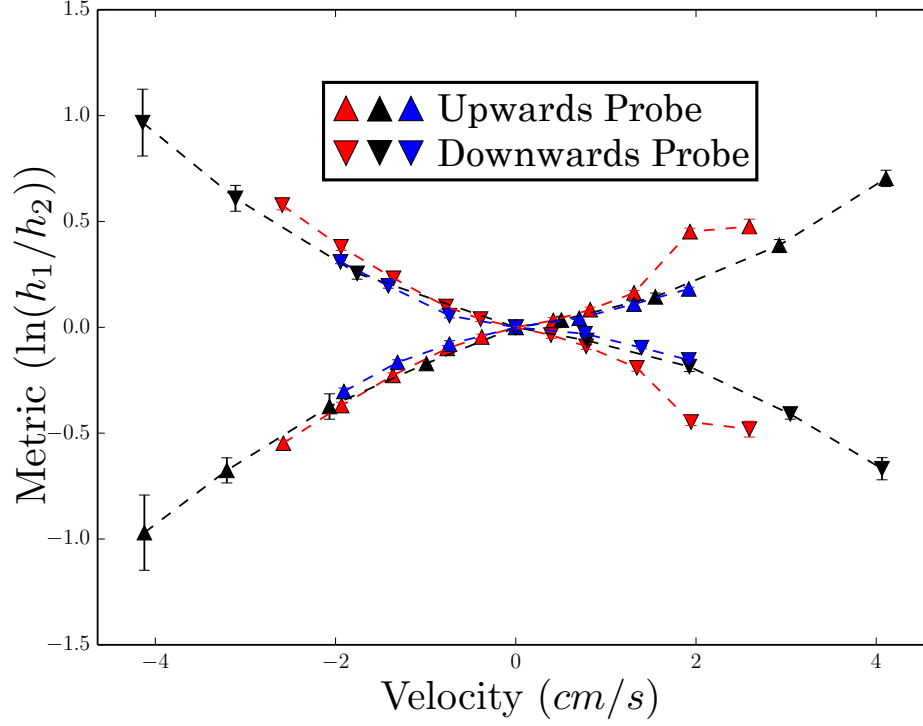


Figure SI.7: Shifted calibration curves for three instances of the sensor reveal a predictable relationship between metric and velocity.

Fig. SI.10 shows the metric as a function of flow velocity for 3 orientations of the calibration tube; horizontal, 45° , and vertical, when the sensor is either parallel or orthogonal (cap windows 90° from tube axis). Negligible change in metric for all orientations in which the sensor was misaligned indicates that the sensor cap effectively rectifies flow for all orientations; any flow component perpendicular to the sensor would have negligible effect on the measured value. When the flow is aligned with the sensor, for the full range of probe and tube orientations, there is only a small shift in the curve. Additionally, Fig. SI.11 shows that a vertically placed sensor's sensitivity to flow decreases to zero as the direction of flow is changed from vertical to horizontal. These rule out the possibility of non-trivial sensitivity to conduit orientation.

Fig. SI.12 shows the metric as a function of probe angle in a vertical tube of constant flow velocity 3.1 cm/s, where the probe is aligned (0°) or orthogonal ($\pm 90^\circ$) to the tube. The good fit to a cosine shows that flows not aligned with the probe (horizontal flows in the field) do not significantly affect the measurement.

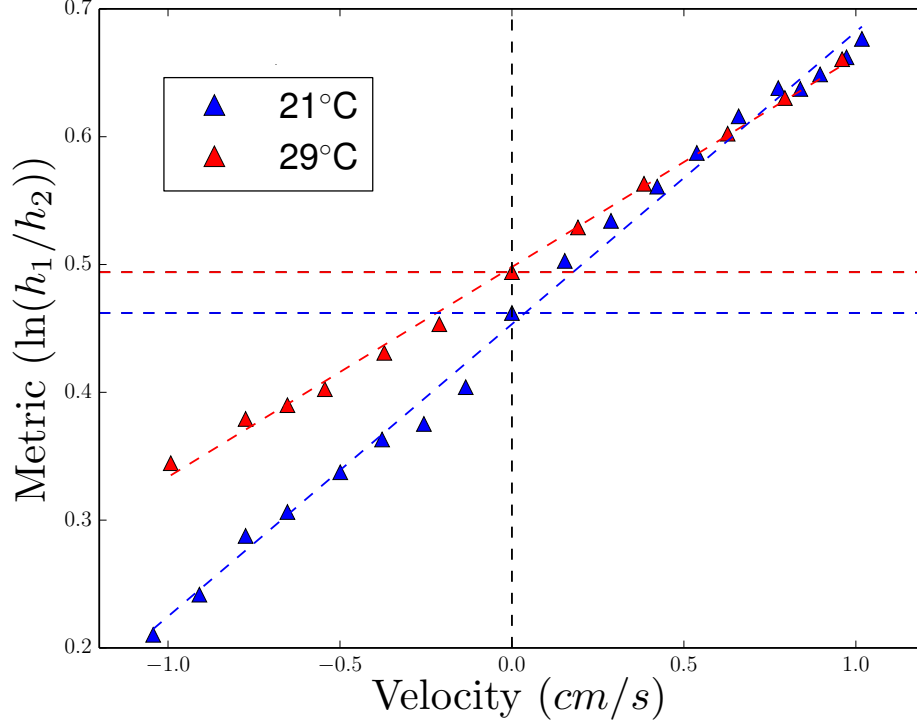


Figure SI.8: Calibration curves for two temperatures show a slight shift ($\sim 0.2\text{cm/s}$) and slope change ($\sim 40\%$) for this temperature difference, which is closely matched with the total range observed in live mounds. Horizontal and vertical lines are to guide the eye.

2 Additional Measurements: Long-term flow in a dead mound

Continuous flow in five flutes from the dead mound were measured, shown in Fig. SI.13. Four out of five flutes follow the observed trend. The heterogeneity is likely due to the complex geometry and is consistent with the few live mound measurements which also go against the trend.

One flute (which happened to go against the observed trend) was measured for three days. For the first two days, the mound (at the edge of a forest) was exposed to partial direct sunlight. It can be seen in Fig. SI.15 that the measured air velocity strictly follows a daily schedule, where fine features repeat themselves. On the third day, a tarp was positioned above the mound, keeping the mound shaded from any direct sunlight, but exposed to ambient temperatures. Some midday features are missing, presumably those directly induced by solar heating, but the general trend remains the same.

3 Permeability Measurements

The mound material is 37–47% air by volume, and has an average pore size of $\sim 5\mu\text{m}$, roughly the mean

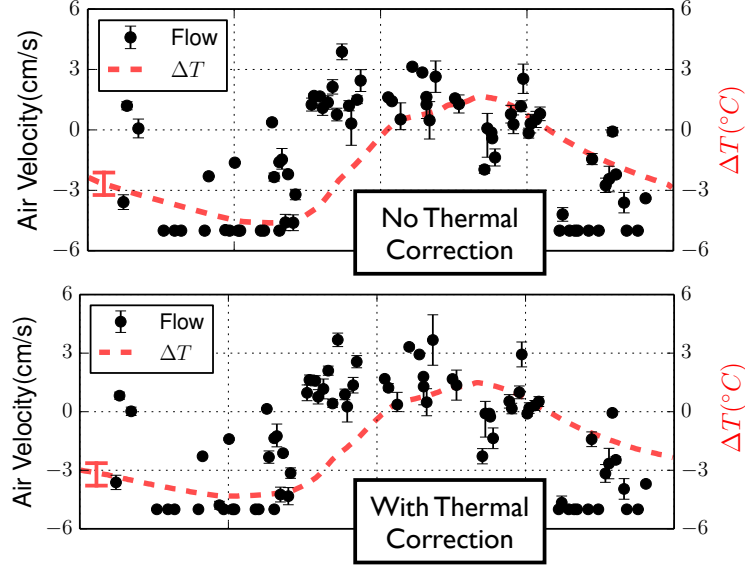


Figure SI.9: Comparison of calculated velocities where temperature-dependent sensitivity is taken into account

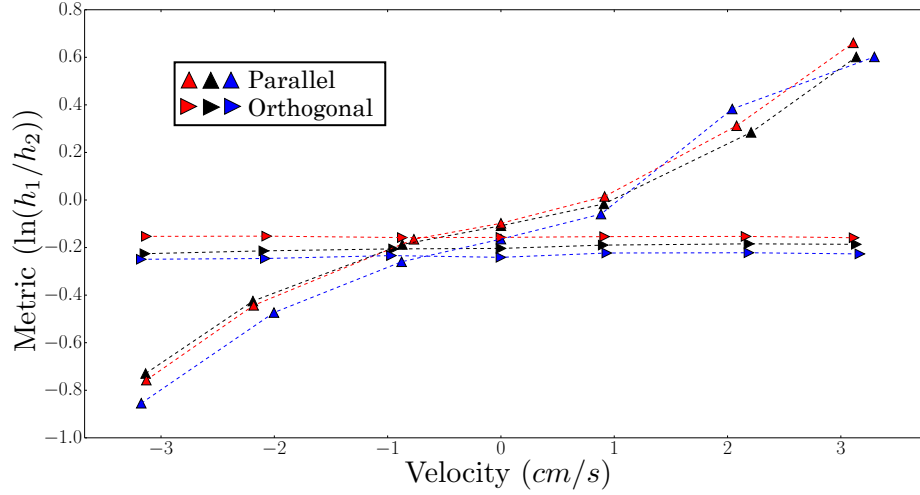


Figure SI.10: Velocity metric as a function of flow speed tube orientation and relative probe orientation. Regardless of whether the tube is vertical (red), diagonal (45°, black) or horizontal (blue), the probe is only sensitive to flow velocity when the probe is aligned parallel with the tube (upwards triangles), and not when orthogonal (rightwards triangles)

particle size [2]. To determine the degree to which this admits bulk flow of air, air was pulled through the tube by a vacuum source, mass flow controller (Alicat MC-20slpm), and conical sample of mound wall sealed

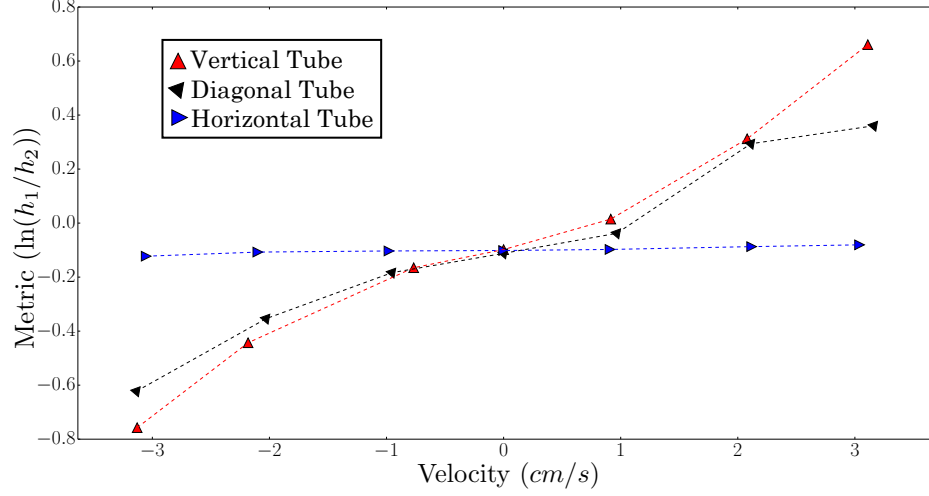


Figure SI.11: Velocity metric as a function of flow speed and tube orientation for a vertical probe. When the tube is vertical(90°), sensitivity is highest, diagonal(45°), gives reduced sensitivity, and the probe is not sensitive to horizontal flows(90°) at all.

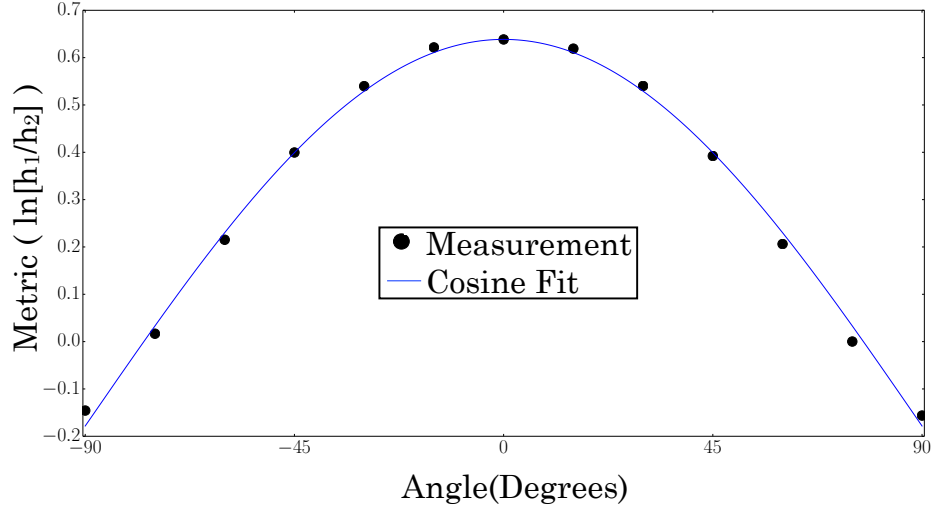


Figure SI.12: Velocity metric as a function of probe rotation in a tube with upwards flow.

with gypsum. In parallel was a piece of glassware inside a water reservoir, connected to the mound sample on top (Fig. SI.15). The height differential Δh allows us to calculate the back pressure $\Delta P = g\rho\Delta h$. This, combined with the measured air flow Q (measured by the mass flow controller) gives the permeability of mound sample $\kappa = Q/(\Delta PA)$, where A is the area of the sample. Our measured values for a larger mound sample are in rough agreement with the measurements [2] on hydraulic conductivity.

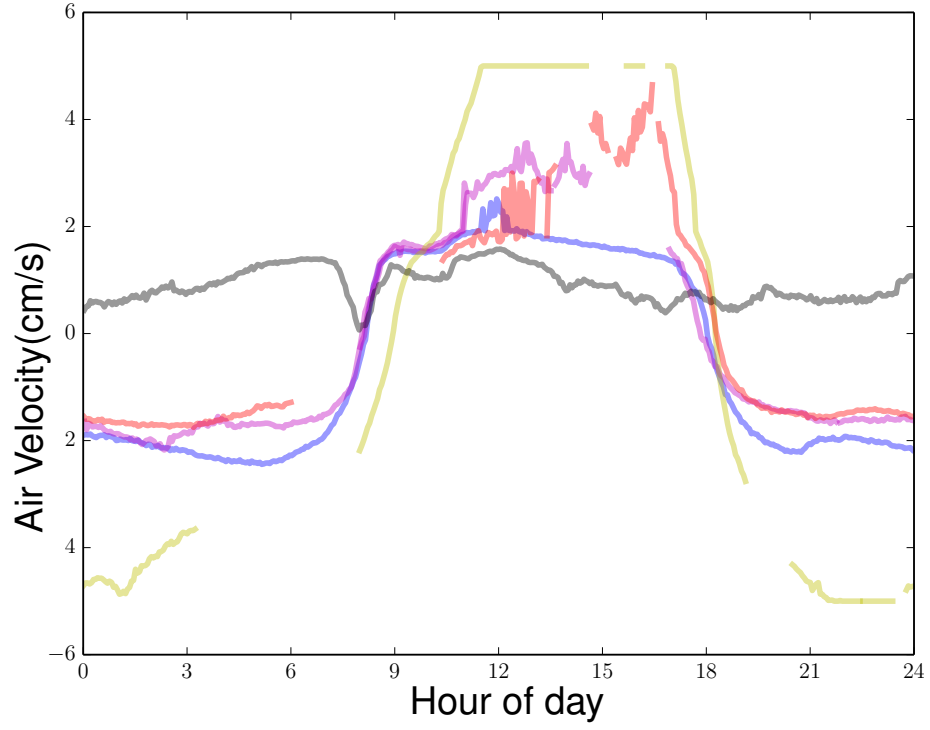


Figure SI.13: Continuous flow measurements of 5 flutes in a dead mound.

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- [2] Kandasami R, Borges R, Murthy T (2015) *in preparation*.

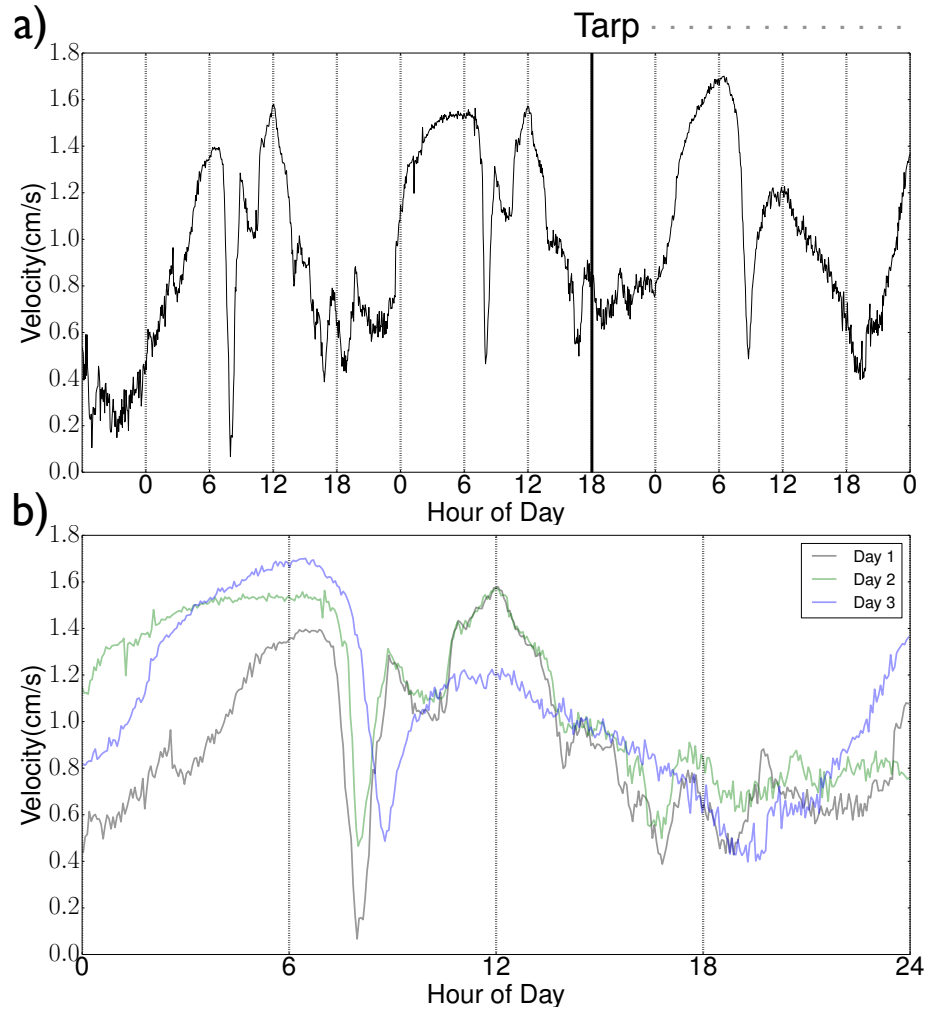


Figure SI.14: a) 3 day flute flow measurement. A tarp was hung to shade the mound on the third day. b) The same data, with days 1, 2, 3 overlaid on top of each other.

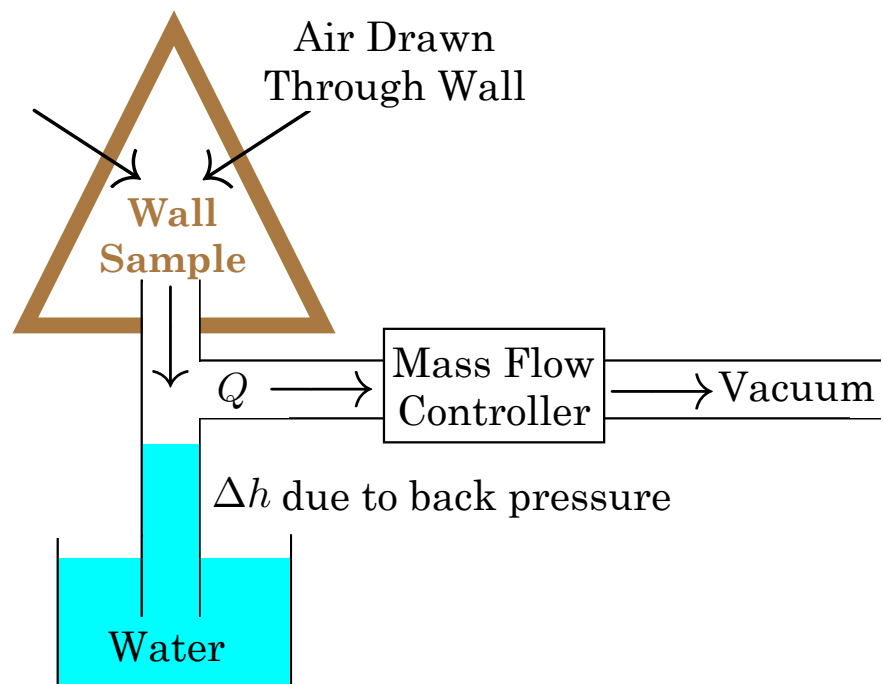


Figure SI.15: Schematic of permeability measurement apparatus.